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Differences in the physiological responses to temperature among stonechats from three populations reared in a common environment

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Abstract

The physiological response to variation in air temperature (T_a) can provide insights into how animals are adapted to different environments. I measured metabolic rate, total evaporative water loss (TEWL) and body temperature (T_b) as a function of T_a in stonechats from equatorial Kenya, temperate central Europe and continental Kazakhstan, environments where stonechats have evolved different life histories. All birds were raised and kept under identical captive conditions to highlight genetically based differences and to exclude phenotypic plasticity as explanatory factor. The slope relating metabolic rate to T_a was steepest in Kazakh stonechats and lowest for birds from Kenya, indicating that, counterintuitively, the tropical stonechats were best insulated. Taking into account variation in T_b in response to T_a, the lower critical temperature for the three populations fell between 32.0 and 34.9 °C, values higher than previously assumed. Whole organism BMR did not differ among populations, but because body mass was significantly higher in the Kenyan stonechats, their mass-specific BMR was lower compared with conspecifics from higher latitude. Whole organism or mass-specific TEWL did not differ among populations. Possibly, Kenyan birds are better insulated to compensate for their limited capacity to elevate metabolic rate.

Keywords: Bird; Metabolic rate; BMR; Body temperature; Total evaporative water loss; Life history adaptation

1. Introduction

To understand how animals are adapted to their environment, traditional emphasis in comparative and ecological physiology has been on energy expenditure in relation to food and temperature characteristics of the environment (Scholander et al., 1950; Bartholomew, 1964; Dawson and Carey, 1976; Bryant et al., 1984). More recently a more holistic approach attempts to combine life history traits and various physiological characteristics, including immunological, endocrinological and metabolic processes, into an integrative perspective on adaptation to the environment (Ricklefs et al., 1996; Hulbert and Else, 2000; Ricklefs and Wikelski, 2002; Tieleman et al., 2005). This approach tries to come to grips with the manifold correlations between various life history and physiological traits by attempting to identify clusters of and connections among traits. Metabolic rate is thought to be a major hub in the network of physiological mechanisms connecting life history traits (Drent and Daan, 1980; Ricklefs and Wikelski, 2002; Wikelski et al., 2003; Speakman, 2005).

When metabolic rate is included in attempts to understand adaptation to environmental conditions – be it as a singular measure or as a component of a more integrative approach – the focus is largely on field (FMR) and/or basal metabolic rate (BMR). The former provides an overall measure of the energetic costs of a 24-h routine of a free-living animal, integrating behavior, thermoregulation and physiology (Nagy, 1987; Speakman, 1997), while the latter is thought to be a clearly defined measure of physiological maintenance costs, relevant because it is related to FMR and life style (Calder and King, 1974; King, 1974; Drent and Daan, 1980; Harvey et al., 1991). The emphasis on FMR and BMR sometimes overshadows a third interesting component of metabolic adaptation, namely the metabolic response to variation in temperature. Whereas tropical and desert species are usually found to have a low BMR, relative to their size, their metabolic response to changes in air temperature (T_a) is less

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predictable. One might predict that they are less insulated in their thermally benign environments (Scholander et al., 1950), and when exposed to cold upregulate their metabolic rate substantially to maintain body temperature (T_b). Conversely, one might hypothesize that their low BMR provides them with a limited capacity to upregulate their metabolism (Bennett and Ruben, 1979; Drent and Daan, 1980; Daan et al., 1990; Ricklefs et al., 1996), and therefore they must either drop their T_b or possess better insulative properties to deal with reduced T_a.

To gain insights into these possibilities, I compared the physiological responses to T_a of three populations of stonechats, originating from different environments, where they have evolved different life history strategies (Gwinner et al., 1995; Urquhart, 2002; Rödl et al., 2004). The difference between the environments can be summarized by their seasonal variation and is reflected in the life cycles of their inhabitants. Kenyan stonechats (*Saxicola torquata axillaris*) are equatorial residents that live in tropical savannahs; Central European stonechats (*S. t. rubicola*) are short-distance migrants that arrive from their Mediterranean wintering areas at their breeding grounds in April for a 6–7 month stay; and stonechats breeding in Kazakhstan (*S.t. maura*) are adjusted to its continental climate with a short summer season by their long-distance migrations and relatively brief, about 3 months, visit to their breeding grounds. The Kenyan stonechats have a long reproductive window, the most protracted molt period, slowest growth and lowest reproductive efforts, whereas the Kazakh birds display the opposite characteristics, and the Central Europeans have mostly intermediate values (Starck et al., 1995; Gwinner et al., 1995; Helm and Gwinner, 1999; Rödl et al., 2004). Related to these life cycle differences, the resting metabolic rates of birds measured at 25–26 °C are lowest in the Kenyan population, both in summer and winter, while the Central European and Kazakh populations are similar in winter and intermediate and highest, respectively, in summer (Klaassen, 1995; Wikelski et al., 2003). Klaassen (1995) found that Kenyan birds had a relatively larger feather mass when compared with European stonechats. Therefore, we might expect that Kenyan birds exposed to T_a below the thermoneutral zone elevate their metabolism less and still maintain T_b, when compared with Central European individuals. Feather mass of Kazakh birds has not been measured, but based on the similarity in metabolic rate at 25–26 °C they might resemble European stonechats in their response to T_a, at least in winter.

I measured metabolic rate, total evaporative water loss (TEWL) and T_b as a function of T_a in stonechats from Kenya, Central Europe and Kazakhstan, and determined the lower critical temperature and BMR. All birds were raised and kept under identical captive conditions. This common garden set up allows us to highlight genetically based differences in the physiological responses to T_a, and excludes phenomena of phenotypic plasticity, such as developmental plasticity and acclimatization, as explanation for differences among populations. The results indicate that stonechats from different environments have evolved different physiological responses to T_a, and in addition point to problems with the findings and interpretation of previous work on the BMR of stonechats from these populations.

2. Material and methods

2.1. Birds

I measured 6–10 individuals from populations of stonechats originating from Kenya (*Saxicola torquata axillaris*), Austria (*S. t. rubicola*) and Kazakhstan (*S. t. maura*). All birds were hand-raised in Andechs, Germany, after being bred in captivity (all but one individual) or being collected in the field as nestling (one Kazakh stonechat) (Gwinner et al., 1995). After fledging they were housed in individual cages under constant temperatures of 20–22 °C and day length conditions mimicking those of Andechs (N48° E11°). Birds were distributed randomly over six rooms. All birds were measured in February and March 2005 during the last part of their winter-phase and the onset of their spring migratory restlessness as determined by nocturnal activity.

2.2. Use of BMR and RMR

Throughout the manuscript I have used the term BMR for the metabolic rate of a post-absorptive, inactive individual measured during the nocturnal phase at thermoneutral temperatures (Calder and King, 1974). RMR refers to the metabolic rate measured under the same conditions, but not at thermoneutral temperatures. It therefore includes thermoregulatory costs.

2.3. Laboratory set up and measurements

I measured rates of oxygen consumption and TEWL for post-absorptive birds during their nocturnal phase by standard flow-through respirometry and hygrometry methods (Gessaman, 1987). Birds were placed in 13.5-L steel metabolic chambers with a Plexiglas lid that was fitted airtight with a rubber gasket. The metabolic chambers were located in a walk-in environmental chamber that controlled $T_a \pm 0.2$ °C. Birds sat on a perch above a wire mesh platform over a layer of mineral oil that trapped feces, thus excluding them as a source of water in the measurements. Oxygen consumption and water content of the air were measured with a positive pressure system: compressed outside air from a tank coursed through columns of silica gel, soda lime and silica gel, to remove water and CO_2 from the air stream. Next, the air stream was split into four tubes with three lines passing through three previously calibrated (Levy, 1964) mass-flow controllers (Brooks, model 5850E) set between 500 and 850 mL min^{-1} (STP) depending on T_a, and then through the three metabolic chambers, while the fourth stream was used to measure inlet air properties. Exiting air passed through a dewpoint hygrometer (General Eastern, M4-DP) before a subsample was routed through silica gel, ascarite and silica gel before entering a dual channel oxygen analyzer (Oxzilla, Sable Systems) to determine the fractional concentration of oxygen in dry, CO_2-free air. I measured birds at different times during the night and at 1–3 different temperatures per night. The first measurements were taken at least 3 h after the beginning of the dark phase. After a three-hour equilibration period, I recorded the oxygen concentration and dewpoint of inlet and outlet air, the temperature of the dewpoint hygrometer, and the T_a in the chamber, using a data

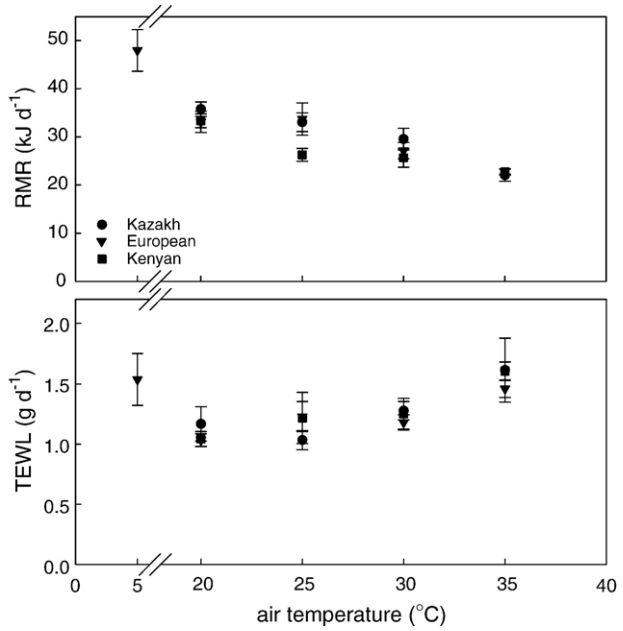

Fig. 1. Average (±1 SE) resting metabolic rate (RMR, kJ d^{-1}) and total evaporative water loss (TEWL, g d^{-1}) as a function of air temperature for Kazakh, European and Kenyan populations of stonechats kept in a common garden situation in Andechs, Germany.

logger (Campbell Scientific, CR23X). When, after the third hour of measurements the traces of oxygen consumption and dewpoint were stable for at least 10 min, I noted these times and used these data for calculations. Although some measurements were made during the annual phase in which birds showed bouts of nocturnal migratory restless, all measurements were made on inactive birds as determined by the trace of O_2-consumption and quietude of the birds in the metabolism chambers. Oxygen consumption was calculated with equation 2 of Hill (1972), and converted to heat production with the factor 20.08 J/mL O_2 (Schmidt-Nielsen, 1997). Evaporative water loss was calculated following Tieleman et al. (2002). Immediately after the completion of the metabolism measurements I measured T_b of birds with a digital thermometer (OMEGA, model ATT) and a 36-gauge copper-constantan thermocouple.

2.4. Statistical analysis

Averages are presented ±1 SD, unless specified otherwise. ANOVA was performed using the GLM-procedure in SPSS 14.0. I always included interaction terms in the initial model, but did not report insignificant interactions. To identify significant differences within factors with three or more groups I used the Tukey HSD test after one-way ANOVA and contrast analysis for multivariate ANOVA.

3. Results

3.1. Body mass

Body mass was lowest in the Kazakh birds (13.6±2.44 g, $n=6$), intermediate in the Europeans (15.3±1.91 g, $n=10$) and highest in the Kenyans (18.8±2.18 g, $n=10$). The difference between populations was significant ($F_{2,\ 23}=12.4$, $P<0.0001$) and a post-hoc test indicated that the Kenyans had a significantly higher body mass than the other two populations (Tukey HSD, both $P<0.005$), which did not differ significantly from each other (Tukey HSD $P=0.30$).

3.2. Resting metabolic rate, total evaporative water loss and body temperature

Whole-organism resting metabolic rate (RMR) decreased with increasing temperature in all three populations (Fig. 1). An ANOVA with RMR as dependent variable and population and T_a as fixed factors revealed that populations did not significantly differ from each other ($F_{2,\ 92}=2.26$, $P=0.11$) but that T_a had a significant influence on RMR ($F_{4,\ 92}=38.67$, $P<0.0001$). Contrast analysis of the type "repeated" showed that RMR at each T_a was significantly different from RMR at the preceding T_a (all $P<0.05$).

Total evaporative water loss (TEWL) varied with temperature in all three populations in a similar fashion, with the highest TEWL-values at the highest T_a (Fig. 1). An ANOVA with population and T_a as fixed factors detected no significant differences between populations ($F_{2,\ 90}=0.47$, $P<0.63$) but a significant effect of T_a ($F_{4,\ 90}=6.83$, $P<0.0001$) on TEWL. Using contrast analysis of the type "repeated" I found that TEWL at 35 °C differed significantly from TEWL at 30 °C ($P=0.003$), but that TEWL at 30 °C, 25 °C and 20 °C did not differ significantly from each other (all $P>0.49$). TEWL at 25 °C, often used in interspecific comparisons, did not differ significantly among populations, whether expressed as whole-organism values or on a mass-specific basis (Table 1, whole-organism TEWL $F_{2,\ 14}=0.46$, $P=0.64$; mass-specific TEWL $F_{2,\ 14}=0.44$, $P=0.66$).

Body temperature for the three populations averaged between 39.7 and 41.2 °C at T_as between 25 °C and 35 °C, but dropped at T_a below 25 °C (Fig. 2). Using ANOVA I found no significant effect of population on T_b ($F_{2,\ 23}=2.66$, $P=0.09$) but a highly significant effect of T_a ($F_{4,\ 23}=16.51$, $P<0.0001$).

3.3. Mass-specific and normothermic metabolic rates

Because T_b varied with T_a, the Newtonian cooling model cannot be fit to the original data in order to determine the lower critical temperature (T_{lc}) and BMR (Scholander et al., 1950). Therefore, I estimated "normothermic RMR" at each T_a as $M_n=E_m+h_m(T_{b\_n}-T_a)$ where E_m is the measured evaporative heat loss (kJ g^{-1} d^{-1},

Table 1
Whole-organism and mass-specific total evaporative water loss rates of stonechats from Kenya, Central Europe and Kazakhstan

Population	TEWL (g d^{-1})±SD	Mass-specific TEWL (mg d^{-1} g^{-1})±SD	n
Kenya	1.22±0.520	67.0±29.68	6
Central Europe	1.23±0.306	77.7±14.63	6
Kazakhstan	1.03±0.178	79.0±25.04	5

assuming that evaporation of 1 g water equals 2.426 kJ evaporative heat loss), the measured dry heat transfer coefficient $h_m = (M_m - E_m)/(T_{b\_m} - T_a)$, and normothermic T_{b_n}=41.1 °C, the average T_b at T_a=35 °C. To calculate h_m I used M_m, the measured metabolic rate (kJ g^{-1} d^{-1}), E_m, the measured evaporative heat loss (kJ g^{-1} d^{-1}), and T_{b_m}, the measured body temperature (°C). For those birds for which I did not measure T_b I used the average T_b for a given population and T_a. In addition, because body mass differed among populations, I calculated mass-specific metabolic rates (kJ d^{-1} g^{-1}) that might provide different insights from those provided by the whole-organism values (Fig. 2). Intersecting linear regression lines through the mass-specific, normothermic metabolic rates at T_a<35 °C with the values at 35 °C yielded T_{lc}-estimates of 34.6, 34.9 and 32.0 °C for the Kazakh, European and Kenyan populations, respectively (Fig. 2).

Metabolic measurements at 35 °C are therefore in the thermoneutral zone of all populations and can be considered basal metabolic rates (BMR, Table 2). Whole-organism BMR did not differ significantly among populations (ANOVA population $F_{2, 37}$=0.27, P=0.77), but mass-specific BMR was significantly lower in Kenyan birds than in European and Kazakh stonechats (ANOVA population $F_{2, 37}$=6.25, P=0.005; Tukey HSD Kenyan vs. European and Kazakh, both P<0.014).

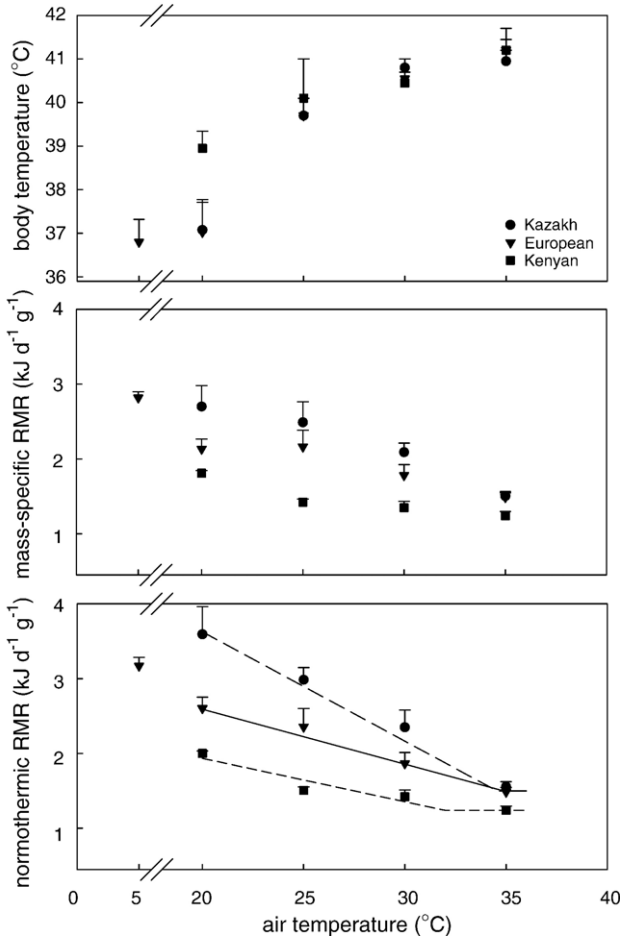

Fig 2. Average (±1 SE) body temperature (°C), mass-specific resting metabolic rate (RMR, kJ d^{-1} g^{-1}) and normothermic mass-specific RMR (kJ d^{-1} g^{-1}) as a function of air temperature for Kazakh, European and Kenyan populations of stonechats kept in a common garden situation in Andechs, Germany. Calculation of normothermic values is explained in the main text.

Table 2
Whole-organism and mass-specific basal metabolic rates of stonechats from Kenya, Central Europe and Kazakhstan

Population	BMR (kJ d^{-1}) ±SD	Mass-specific BMR (kJ d^{-1} g^{-1})±SD	n
Kenya	22.7±2.36	1.24±0.209	14
Central Europe	22.8±2.19	1.49±0.229	15
Kazakhstan	22.0±4.14	1.50±0.206	11

For each population, 5 individuals were measured twice, the other individuals once.

4. Discussion

The physiological response to a range of T_a, as measured by the combination of metabolic rate, TEWL, h and T_b, differed among Kenyan, Central European and Kazakh stonechats when body mass was incorporated into the comparison. The slope relating normothermic metabolic rate to T_a (in (kJ d^{-1} g^{-1})/°C) was steepest in the Kazakh stonechats (−0.146±0.032 (SE)), intermediate in the birds from Central Europe (−0.074±0.023 (SE)) and lowest in the Kenyan population (−0.058±0.010 (SE)). This finding resonates with Klaassen's (1995) data that plumage mass was 18% higher in Kenyan stonechats than in European stonechats, and confirms that the Kenyan birds are best insulated. Taking into account differences in body mass among populations and variation in body temperature in response to T_a, the lower critical temperature of stonechats was 7–10 °C higher than previously assumed (Klaassen, 1995) or suggested (Wikelski et al., 2003). These results emphasize the need to measure all components of the heat balance, including T_b, before fitting a Newtonian cooling model to identify thermoneutral temperatures at which to measure BMR.

At the whole-organism level BMR did not differ between populations, but because body mass was significantly higher in the Kenyan stonechats, mass-specific values were significantly lower in these tropical birds than in their conspecifics from higher latitudes. This pattern resembles findings of a recent intraspecific comparison of tropical and temperate zone house wrens (*Troglodytes aedon*), that also have a larger body mass, identical whole-organism metabolic rate, and lower mass-specific metabolic rates in the tropical forms than in their temperate zone counterparts (Tieleman et al., 2006). The larger body size of the tropical stonechats and wrens goes against Bergmann's rule that predicts increasing body size with latitude (Blackburn and Gaston, 1996; Ashton, 2002). An environmental factor often related to BMR (and FMR and body mass) is food availability (e.g. Dawson, 1984; McNab, 1988; Williams et al., 2004). If food availability is lower in the tropics (e.g. Foster, 1977; Martin, 1987), then one would predict lower whole-organism metabolic rates in tropical birds. However, the identical whole-organism metabolic rates suggest that food is not a selective factor of overruling importance for metabolic rates of tropical stonechats. Instead, the reduced mass-specific values could indicate that slower aging and lower intrinsic

mortality are important selective factors in the tropics (Speakman, 2005; Tieleman et al., 2006).

When I compare BMR of these stonechats with allometric predictions, values for Central European birds were 6% higher, for Kenyans 11% lower, and for Kazakh 7% higher than predicted for their respective body masses (Tieleman and Williams, 2000). To compare my measurements at 25 °C with previously published values, I read averages from Klaassen's (1995) Fig. 1 and Wikelski et al.'s (2003) Fig. 2 (using the intended units of mL O_2/h/g instead of the published units of mL C_2/min/g, Wikelski pers. comm.). Klaassen's (1995) values were within the same range as my measurements with averages about 9% and 18% lower for the Kenyan and European birds, respectively, while Wikelski et al. (2003) reported values 42–49% lower. Major differences between the current study, Klaassen (1995) and Wikelski et al. (2003) are metabolic chamber size (13, 9.7 and 36 L, respectively) and flow rate (500, 200 and 900 mL/min, respectively). Wikelski (pers. comm.) suggests that the smaller chambers might be more stressful to the birds causing a different physiological state and higher metabolic rates. Alternatively, the combination of large chamber size and high flow rate leads to increased washout times and results in low delta O_2-values (0.1–0.24% in the current study, 0.27–0.45% based on Fig. 1. in Klaassen (1995) and 0.03%–0.05% based on winter data in Fig. 2 in Wikelski et al., 2003), increasing measurement error.

The reduced slope relating metabolic rate and T_a, the low BMR and the better insulative properties of Kenyan stonechats, raise questions about the evolutionary mechanisms that might explain these patterns. It is unlikely that Kenyan stonechats experience more cold temperatures in the field than their Kazakh and European counterparts. The low slope relating metabolism and T_a is therefore probably not the direct selective effect of exposure to cold. A more likely scenario is that the low BMR is functionally related to a reduced working capacity, in accordance with their small brood size, and results in a low thermoregulatory capacity. The better insulation is then an adaptive byproduct for the need to thermoregulate in the absence of a large capacity to elevate metabolic rate. Similar findings in a comparative study on larks from arid and mesic areas, with lower BMR and better insulative properties in the arid-zone species (Tieleman et al., 2002), could be explained likewise. This logic results in the testable prediction that maximum metabolic rate, either through cold exposure or through locomotion, is lowest in the Kenyan stonechats compared with the other populations.

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